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Cropping of Sea Anemone Tentacles by a Symbiotic Barnacle

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As sessile animals, barnacles (Cirripedia: Thoracica) are generally suspension feeders, extending their cirri into the surrounding water to collect food particles (1). Although it has been suggested that some symbiotic barnacles obtain nutrients directly from their hosts, either by absorbing body fluids (2–4) or by rasping the host's tissue (4–6), most of these cases are inferred from their morphology. Direct evidence, such as gut content analysis, has been limited (for an exception, see ref. 5), and no actual feeding on their hosts has been observed. Koleolepas avis *(Hiro, 1931) is a pedunculate barnacle symbiotic with the sea anemone* Calliactis japonica, *which lives on gastropod shells occupied by large hermit crabs (7), mainly* Dardanus arrosor. *Symbiotic relationships between various hermit crabs and sea anemones have been well documented (8), but the relationship between the barnacle and its host sea anemone has been virtually unknown. From February to April 1996, we collected living individuals of* K. avis *from lobster nets landed at Minabe Fishery Port, southwestern Japan (33° 44′ N, 135° 20′ E). On the basis of behavioral observations in the laboratory and analyses of fecal pellets and gut contents, we concluded that this barnacle feeds actively on its host's tentacles.*

The shape of *Koleolepas avis* (Fig. 1) differs from that of typical pedunculate barnacles like *Lepas* spp. in many ways (7). First, *K. avis*, like its two congeners *K. willeyi* Stebbing (9) and *K. tinkeri* Edmondson (10), has a sheath-like structure extending from the base of the peduncle and covering the main body (the attachment disk). Second, at the orifice, *K. avis* has a chitinous, bill-like projection that is developed only in this species. Hiro (7) stated that this projection gives "the cirriped a bird-bill-shape." These two characteristics are reflected in the generic and specific names, respectively ("koleo" means sheath and "avis" means bird). Third, the peduncle is highly distensible, being about three times as long as the length of the capitulum. In addition to these external characteristics, the internal morphology is also distinct. The cirri are short, with sparse setae, and thus unsuitable for filter feeding, and the cutting edge of the mandible is peculiarly serrate (7).

Observations on living individuals showed that the attachment disk of *K. avis* was interposed between the pedal disk of its host anemone and the gastropod shell. Most of the barnacle's main body was retracted into the attachment disk, and only the upper part of the capitulum was visible from outside of the host (Fig. 2A). A rhythmical cirral movement could be seen through the semitransparent capitulum, but otherwise the barnacle usually remained motionless.

When tentacles of the sea anemone touched *K. avis* (presumably its cirri), the capitulum of the barnacle immediately came out from the gap under the host and began to follow the tentacles (Fig. 2B). This tentacle-following behavior lasted 89 ± 122 s (mean ± SD of 46 observations on 10 individuals). During this period, the cirri were widely spread and almost motionless. When the cirri of *K. avis* touched a tentacle of its host again, the barnacle grabbed it with its cirri, pulled part of it into the capitulum, and closed the orifice firmly. At the same time the peduncle shrank and bent frontally (to the direction of the orifice). As a result, the tentacle became pinched by the upper ridge of the bill-like projection of *K. avis* (Fig. 2C). In response to the pinching, the sea anemone contracted its tentacles. Pulled from the both ends, the pinched tentacle tore off (Fig. 2D). This tentacle pulling lasted 109 ± 95 s.

A barnacle cropped a tentacle 1.4 ± 1.4 times a day (mean ± SD of 10 individuals). We did not observe the barnacles eat other parts of the host, nor other possible foods

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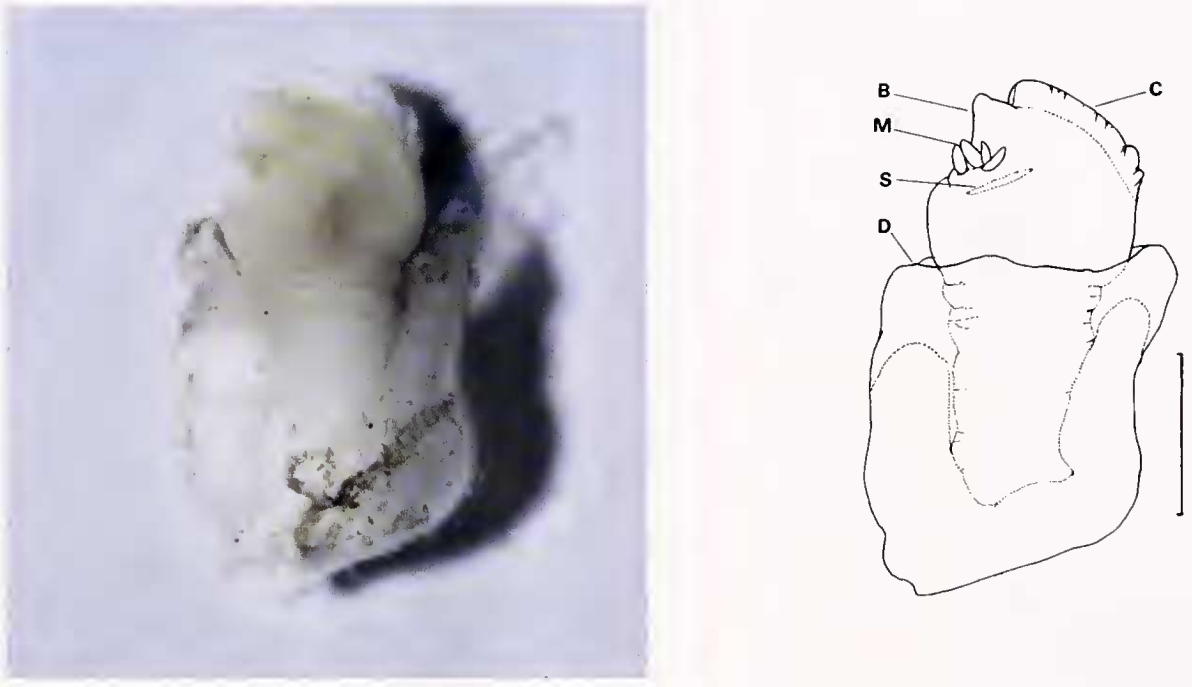

Figure 1. *Koleolepas avis*, viewed from shell side. B, bill-like projection surrounding the orifice; C, crest-like projection; D, attachment disk; M, complemental males (five males, including the one on the other side, are attached to this specimen); S, scutum. Scale bar, 5 mm.

such as living *Artemia* larvae, minced mysids, or commercial fish meal, all of which were readily eaten by *Lepas* spp. (pers. obs.). Fecal pellets of *Koleolepas* were cream white, a color similar to that of its host's tentacles. When observed under a microscope, the pellets were filled with nematocysts. We also found nematocysts in 80% (12/15) of the guts of newly collected barnacles. The guts of the remaining barnacles were almost empty, probably because they could eat little after the snail shells on which they lived were trapped in lobster nets.

The relationship of *K. avis* to the host anemone can be best regarded as parasitic. We did not quantify detrimental effects on the host, mainly because the number of specimens was too small to conduct such a study. However, up to six barnacles per host (pers. obs.) may have some effects on the host, as reported for other parasitic arthropods that feed on their host anemones [a shrimp (11) and a pycnogonid (12)]. Experiments with hermit crabs are necessary to test this assumption, because the presence of hermit crabs may change the frequency with which the barnacles crop anemone tentacles.

Koleolepas avis is the only barnacle known to eat sea anemones, although two other species of barnacles have been reported to eat cnidarian prey (4, 5, 13, 14). Among cnidarian-eating barnacles, *Lepas anserifera* feeds on neustonic medusae as one of many food items (13, 14), whereas *Hoekia monticulariae*, a balanomorph barnacle symbiotic with corals, seems to feed only on its host (4, 5). However, the feeding behavior of *H. monticulariae* is much less active than that of *K. avis:* that balanomorph barnacle is believed to rasp the host's tissue (5) and possibly absorb body fluids of the host coral (4).

The morphological characteristics of *K. avis* are related to the tentacle feeding. First, the bill-like projection of *K. avis* functions like a bill in pinching a long prey. The other two species of *Koleolepas* (the only genus in the family Koleolepadidae) also occur on gastropod shells that are carrying sea anemones and are occupied by hermit crabs (9, 10). However, these species apparently do not have bill-like projections, suggesting that they may have adopted a different feeding habit. Second, the long distensible peduncle is used to follow a tentacle of the sea anemone. Third, the attachment disk allows the peduncle to move freely under the pedal disk of the sea anemone. Finally, its short cirri and peculiar mouth parts are specialized for grabbing and chewing tentacles. A similar specialization is reported in *Hoekia monticulariae*, a coral-eating barnacle: the cirri are strongly reduced and the mandible is modified as a sawlike blade (5).

Whereas tentacle cropping by *K. avis* is a highly unique behavior, it consists of behavioral components common among other pedunculate barnacles: cirral activity, closure of the orifice, elongation and sudden shortening of the peduncle (1). In *K. avis*, the morphology and behavioral components are modified to specialize in cropping the host's tentacles and to live under sea anemones.

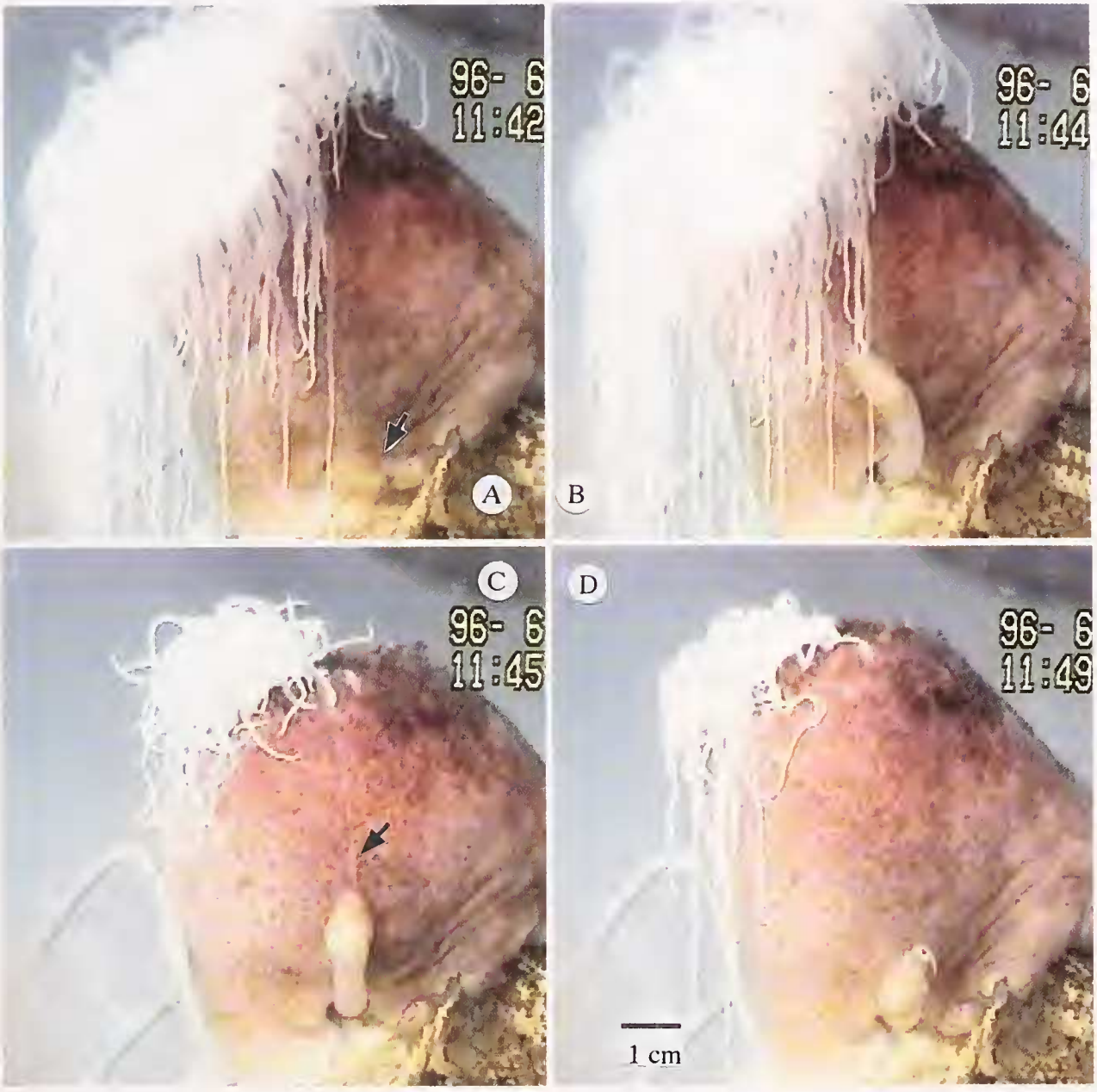

Figure 2. Tentacle cropping behavior by *Koleolepas avis:* (A) Barnacle in resting position (arrow); (B) elongation of the peduncle to follow sea anemone tentacles; (C) pinching a host tentacle (arrow); (D) after cutting off the tentacle, part of which hangs from the orifice of the barnacle. The barnacles and sea anemones were kept in an aquarium with running seawater (symbiotic hermit crabs were removed from the gastropod shells). The sea anemones were fed with minced mysids or commercial fish meal. A fluorescent light (20 W) was used throughout the observations, together with the natural light. The behavior of the barnacles was recorded with a time-lapse video recorder.

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